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Morphological convergence in conifer-dwelling passerines

Received: 19 January 2004 / Revised: 9 February 2004 / Accepted: 9 February 2004 / Published online: 13 March 2004
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Abstract We tested for morphological convergence in conifer specialists among 88 passerines belonging to seven different phylogenetic lineages by discriminant factor analysis. We found a parallel trend among the seven lineages in body mass and digital pad morphology, whereas no such trends existed for the feeding and flight apparatus. Compared to the control species, the conifer specialists have smaller body masses and higher digital pads with maximal widths lying more distally within each of the seven lineages. These traits are interpreted as adaptations to dwelling among coniferous needles.

Keywords Coniferous specialists · Ecomorphology · Morphological convergence · Multivariate analysis · Passerines

Introduction

The hypothesis of convergence states that under similar environmental conditions, species have become more similar in certain characteristics than their ancestors (Schluter 1986). Such similarities, e.g. in morphology, are caused by common selection pressures (Grant et al. 1976; Cody and Mooney 1978; Futuyma 1998). This is an extension of the more general hypothesis that morphological characteristics of organisms are predictable from features of their environment (Hespenheide 1973;

Karr and James 1975; Leisler and Winkler 1991; Ricklefs and Miles 1994).

Convergence should be particularly widespread in groups of animals which are morphologically constrained, e.g. by the requirement of flight as in birds, (Sibley and Ahlquist 1983). Ecomorphological studies in birds have demonstrated that subtle differences in shape of external morphology can have profound ecological effects (Leisler and Winkler 1985, 2001, 2003).

Here we examine possible morphological convergence of passerines living in conifers, adopting a relatively general view of convergence that also includes parallelism (Futuyma 1998). Specifically, we investigate whether a special habitat, i.e. the outermost twigs of temperate conifers (*Pinus*, *Picea*, *Abies*, *Tsuga*, *Larix* and *Pseudotsuga*), has induced the convergence of traits. This microhabitat is inhabited by bird species from seven different phylogenetic lineages. Each lineage is defined by one genus (*Sitta*, *Parus*, *Regulus*, *Phylloscopus*, *Carduelis* and *Carpodacus*), except that we consider two closely related genera (*Dendroica* and *Parula*) as one lineage (Parulidae). Within each lineage, we compare the conifer specialists with congeneric species inhabiting various other habitats.

So far, the relationship between morphology and coniferous habitat has only been compared within genera and has often yielded contradictory results. Within 16 *Dendroica* warblers of North America, the coniferous forest breeders are generally larger than deciduous forest breeders (Greenberg 1979). In contrast, among the Old World *Phylloscopus* warblers, the conifer-dwelling species have significantly lower body masses than the deciduous inhabitants (Gaston 1974; Forstmeier et al. 2001).

Considering the relationship of shape variables and life style we had the following expectations for each of the three functional complexes (feeding apparatus, flight apparatus, and hind limb):

1. A narrow and long bill is an adaptation to probing between needles, as suggested for the golden-crowned

Communicated by: F. Bairlein

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- kinglet (*Regulus satrapa*; Keast and Saunders 1991), and for conifer-dwelling tits (Suhonen et al. 1994).
2. Long and pointed hand wings, broad arm wings and a deeply forked tail characterise frequently hovering species (Norberg 1990). We expect needle-dwellers to be adapted to hovering, because bipedal locomotion is impeded by needles. Increased frequencies of hovering have been shown for coniferous *Phylloscopus* warblers (Gaston 1974).
 3. Two different extremes of locomotion types might induce two different morphological adaptations in the hind limb. Strong, well curved claws are expected for species that use their feet like pliers while gripping twigs or a bundle of needles, or while hooking into cones. Thereby, the centre of the body often hangs upside down, below the contact points of the substrate and the feet. This locomotion type is described for coal tits (*Parus ater*) by Löhrl (1974). On the other hand, plantar integument that provides high friction on thin, smooth structures, and large feet and legs are needed by those birds that cling to the substrate in order to maintain an upright position of the body (Leisler et al. 1989; Winkler and Bock 1976). This locomotion type is typical in thin vertical structures, as for example in reeds (reed warblers *Acrocephalus* sp.; Leisler et al. 1989). A similar locomotion type has been described for the needle-dwelling goldcrest (*Regulus regulus*; Leisler and Thaler 1982). These authors assumed that high friction could be achieved by elevated digital pads.

The objective of this study is to determine the degree of morphological convergence in birds that forage in the outermost twigs of conifers by comparing the morphology among and within lineages.

Methods

Species and specimens

We looked world wide for passerines that forage in the outermost twigs of conifers, and which have one or more congeneric species with a different ecology. We found 28 such species, which we refer to as "needle-dwellers". The congeneric "control species" were selected so that the entire ecological spectrum of each genus was represented in the sample. In order to achieve such a selection, we first defined 13 habitat types that were used for foraging (Table 1). Then, we assigned each congeneric species of each needle-dweller to one or more foraging habitat types. From each genus, we then selected at least one species from each habitat type. If possible, we discarded the rare species. Finally, we added one to three species that showed the most genus-typical foraging habitat. In total, we selected 88 species (Appendix), among them 28 needle-dwellers and 60 control species.

In total, 656 specimens were measured, with an average of seven specimens per species (Appendix). In each species, the sexes were about equally represented.

The study skins were kindly provided by Anatoly Shapoval (private collection, Rybachy), the British Museum of Natural History, Tring, Museum Alexander Koenig, Bonn, Museum für Naturkunde, Berlin, Natural History Museum, Bern, Natural History Museum, Basel, and the Zoological Museum of the University of Zurich.

Table 1 Bird foraging habitat types used for the species selection

Code	Description
1	Coniferous needles, foliage of conifers (i.e. Pinacea)
2	Coniferous twigs, canopy of conifers (i.e. Pinacea)
3	Tree trunk
4	Deciduous foliage
5	Deciduous twigs, canopy of deciduous trees
6	Tree foliage, deciduous or coniferous
7	Tree canopy, deciduous or coniferous
8	Bushes
9	Herbs, grass
10	Ground, sand, steppe
11	Rock
12	Reed
13	Air

Morphological measurements

The study skins were relaxed in airtight boxes which contained pieces of leaves of cherry laurel (*Prunus laurocerasus*; Wechsler et al. 2001). The gas escaping from these leaves contains cyanogenic glycosides that soften dried organic parts.

The following external measurements were taken from the softened skins. From the feeding apparatus: (1) bill length (from the skull), (2) maximum bill depth, (3) maximum bill width (at the gape), (4) maximum length of rictal bristles; from the flight apparatus: (5) length of primary 8, (6) length of primary 10, (7) primary projection (distance from the wing tip to the outermost secondary), (8) distance from the wrist to the tip of 5th secondary, (9) distance from the tip of the alula to the wing tip, (10) distance from the tip of primary 10 to the wing tip, (11) wing length, (12) emargination of the outer web of primary 8, (13) tail length, (14) depth of tail fork (tip to innermost tail feather), (15) graduation (tip to outermost tail feather); from the hind limb: (16) tarsus length, (17) tarsus width, (18) tarsus depth, (19–22) length of digits I to IV (without claws), (23–26) claw length I–IV, (27) curvature of claw I, (28) maximum width of the proximal pad on digit I, (29) length of the proximal pad on digit I, (30) height of the proximal digital pad on digit I, (31) position of max. width in percent of the pad length, (32) foot span without claws, and (33) number of papillae on the proximal pad on digit I.

For the curvature of the claw (27), photographs showing a side view of the hind toe were taken, printed, and the circle formed by the outer edge of the claw was drawn by hand. Then, the angle spanned by the claw was measured in degrees (Feduccia 1993). For counting the number of papillae on the proximal pad on digit I (33), we used a magnifying glass (10×). All measurements were done by the same person (F.K.). In order to capture the amount of variance caused by measurement errors, we measured a selection of characters three times and calculated the percent measurement errors of the variance (Bailey and Byrnes 1990). The proportion of variance caused by measurement error ranged from 2.5% (length of primary 10) to 12.5% (length of the proximal pad on digit I) of the total variance. These errors of individual measurements can be neglected, since species means of each measurement were used for the study.

We used body masses given in Dunning (1992) and complemented them by the handbooks given in the Appendix. For the Vietnamese greenfinch (*Carduelis monguilloti*), we did not find any information on body mass; therefore we estimated its body mass by the regressions of body mass on wing and tarsus length for the other *Carduelis* species.

Statistical analysis

Data transformation

All lengths were corrected for body size by dividing them by the cube root of body mass (Leisler and Winkler 1991). In order to

assess the sensitivity of the analysis to the method of size-correction, we performed all analyses with standardised residuals from the regression of each variable on the logarithm of body mass, as well as with uncorrected variables. The results were the same for all three variable treatments. After the size correction we ln-transformed the variables. We used the arcsine square root transformation for the curvature of the claw (27) and the position of the maximum width of the proximal pad on digit I (31). Finally, the number of papillae (33) was divided by the square of the cube root of body mass and root transformed. Body mass itself was ln-transformed. The Q-Q-plots of the transformed variables showed no large deviation from the normal distribution.

Variable reduction

In order to avoid meaningless significances, the number of variables should not exceed one third of the sample size. Furthermore, the result of the discriminant factor analysis can be strongly affected if the variables are correlated. Therefore, we reduced the number of variables by omitting the ones that had similar loadings in principal component analysis performed for related subsets of the variables separately (Fig. 1). Variables that build clusters in the loading plots can be interpreted as being correlated or redundant. Therefore, only one variable of such a cluster was retained for analysis. In this way, we discarded seven variables: distance from the wing tip to the distance of the alula (9), distance from wing tip to primary 10 (10), length of primary 8 (5), digit 4 (22), foot span (32) and claw 2 and 4 (24,26). The remaining 27 variables were used for the further analysis.

Discriminant function analysis

The ecomorphological analysis of convergence involved two discriminant factor analyses (DFA) on SPSS 8.00 for Windows. First, we separated the phylogenetic lineages from each other, while in the second, the needle-dwellers were separated from the control species. The first DFA was performed to characterise the morphological differences which are due to phylogenetic origin and due to adaptations common to the species within each genus. The aim of the second DFA was to find morphological traits, which characterise needle-dwellers over all seven phylogenetic lineages. Therefore, such traits would indicate convergence. For both analyses, we used a stepwise model selection minimising Wilk's lambda, which is the ratio of the within-group sum of squares to the total sum of squares. In order to test the discriminant functions for robustness, we performed cross-validations, in which species are omitted one at a time before recalculating the discriminant functions. Additionally, we performed a randomisation test for the discrimination between needle-dwellers and control-species by splitting the species 999 times randomly into two groups, keeping the ratio between the groups in each lineage equal to the ratio between needle-dwellers and control-species in our sample. From every randomly grouped sample, we calculated the discriminant functions, as we did for the original sample. Based on these discriminant functions, we calculated the standard distances (distance between the two means divided by the standard deviation) between each of the 999 pairs of random groups. From the distribution of these standard distances we obtained the probability of the observed standard distance (between needle-dwellers and control species). This test gives the probability for the null hypothesis that the observed difference

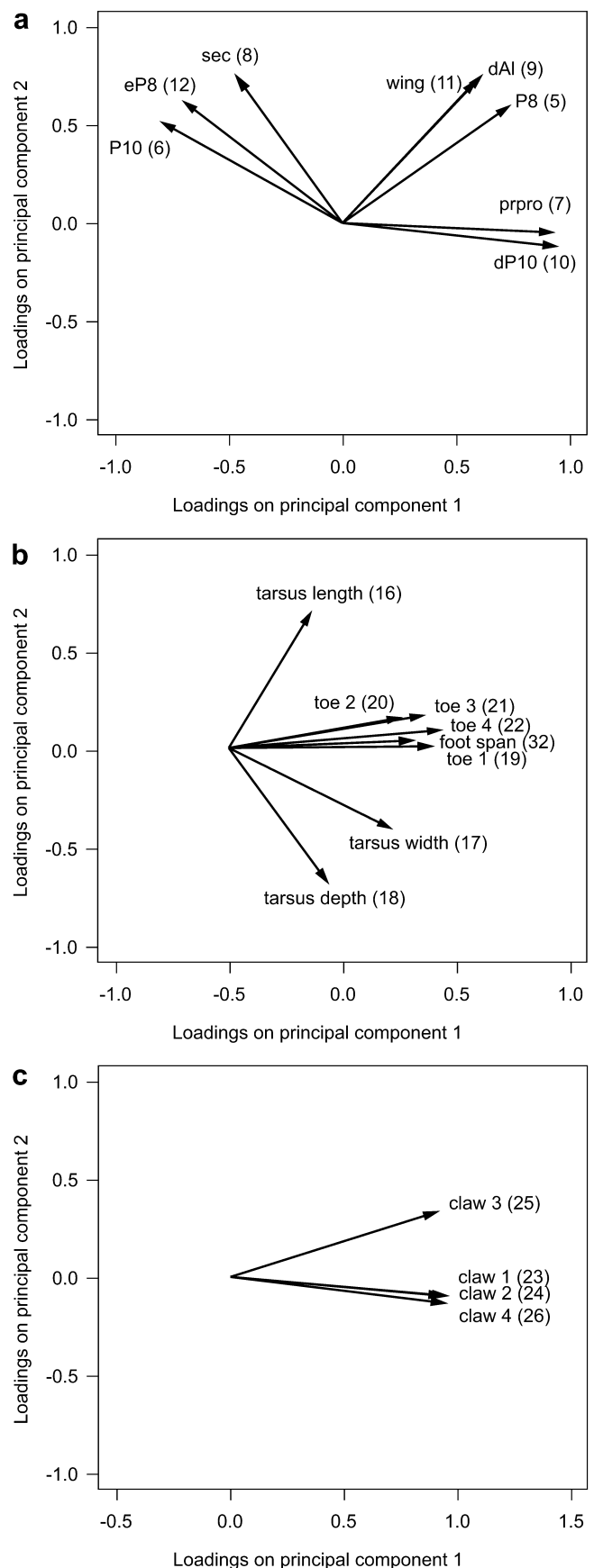


Fig. 1 Loading plots for the first two principal components: **a** of the wing measurements (PC 1: $\lambda = 4.499$, 56.23% of variance; PC 2: $\lambda = 2.789$, 34.86% of variance), **b** of digit lengths and foot span (PC 1: $\lambda = 4.789$, 59.56% of variance; PC 2: $\lambda = 1.239$, 15.49% of variance), and **c** of claw lengths (PC 1: $\lambda = 3.696$, 92.40% of variance; PC 2: $\lambda = 0.151$, 3.77% of variance). Measurements that are correlated lie close together. Numbers correspond to the measurements described in the Methods section

between our groups is a random effect. The randomisation test was performed on R 1.5 (R Development Core Team 2002). In this test, the number of degrees of freedom is too high, since all the 88 species contribute to it, instead of only the seven phylogenetic lineages or the about 20 pairs of sister species containing one needle-dweller and one control species. This might cause that biologically meaningless differences become statistically significant. On the other hand, by combining seven distantly related genera in one analysis, only the largest and therefore biologically most meaningful differences will be detected. We have therefore accepted a number of degrees of freedom which is too high.

Results

The separation of the seven lineages fully succeeded with six discriminant functions ($P < 0.001$ for all six functions). 100% of the species can be correctly grouped, 98.9% by the cross-validated discriminant functions. The first two discriminant functions account for 82.2% of the variance (52.2 and 30.3%, respectively). The species scores for these two discriminant functions are shown in Fig. 2. Eleven variables significantly contribute to the discrimination of the phylogenetic lineages (Table 2). Second DFA separated the needle-dwellers from the control species (Wilk's lambda = 0.78, $df = 3$, $P < 0.001$). This discriminant function contains the variables that commonly characterise the needle-dwellers in our sample. 73.9% of the species can be grouped correctly by the discriminant function, and 71.6% by the cross-validated functions. Three variables significantly contribute to the discrimination, namely the position of the maximal width on the large pad on the hind toe, the height of this pad, and the body mass (Table 3). The standard distance between needle-dwellers and the control species is 1.116, which is exceeded by only 27 of the 999 random samples (Fig. 3). In conclusion, our

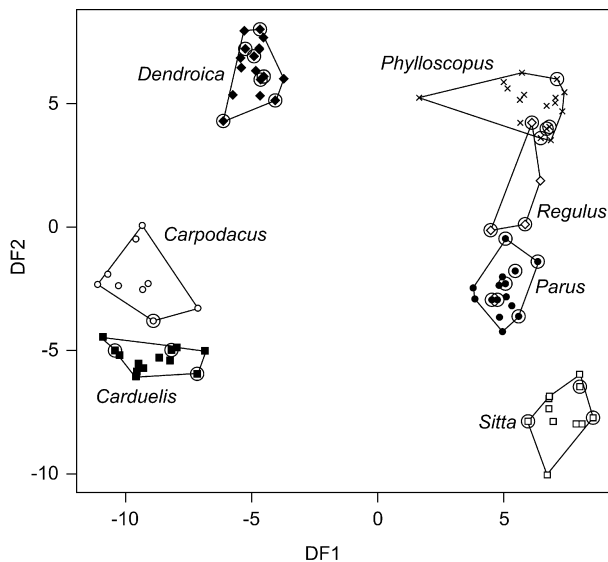


Fig. 2 Scatterplot of the species scores for the first two discriminant functions that separate the taxonomic lineages from each other. Large circle needle-dweller

Table 2 Discrimination of the lineages: Standardised canonical discriminant function coefficients (first number) and within-groups correlations between the variables and the discriminant functions (second number) for the first two discriminant functions. Significant ones are in bold. The variables are ordered as they entered into the discriminant functions

Variable	Discriminant factor 1		Discriminant factor 2	
Length of primary 10 (6)	0.93	0.79	-0.29	-0.13
Tarsus length (18)	-0.10	0.24	0.77	0.44
Length of pad (29)	-0.18	-0.01	0.15	0.41
Depth of tail fork (14)	-0.22	-0.18	-0.12	-0.13
Bill length (1)	0.19	0.18	0.28	0.14
Number of papillae (33)	0.14	0.01	0.44	0.47
Bill depth (2)	-0.55	-0.34	-0.40	-0.27
Length of hind toe (19)	0.22	0.19	-0.46	-0.11
Length of hind claw (23)	-0.11	0.16	-0.48	-0.17
Tail length (13)	-0.12	0.02	0.32	0.19
Width of pad (28)	-0.02	-0.02	0.01	0.12

Table 3 Discrimination of needle-dwellers from the control-species: Standardised canonical discriminant function coefficients and within-groups correlation between the variables and the discriminant function. Significant ones are in bold. The variables are ordered as they entered into the discriminant functions

Variable	Standardised coefficients	Correlation with discriminant function
Body mass	-0.60	-0.55
Position of max. width on toe pad (33)	0.52	0.70
Height of toe pad (30)	0.48	0.66

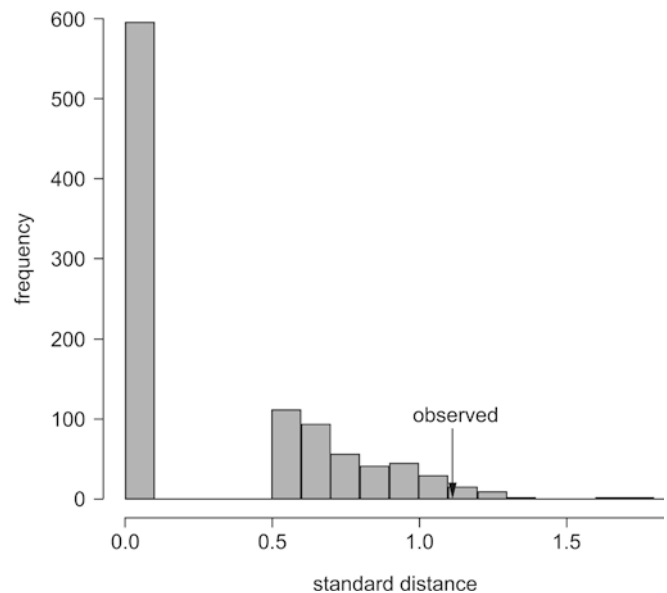


Fig. 3 Distribution of 999 standard distances between pairs of random groups, and the position of the standard distance between the needle-dwellers and the control species. The significance of the null hypothesis "the observed standard distance stems from random groups" is $P = 0.028$

discriminant function did not originate by chance ($P=0.028$), and the convergence seen in Fig. 4 has a significant meaning.

Discussion

Convergence may affect the general appearance of an organism, i.e. its overall morphology (e.g. the diving petrel *Pelecanoides urinatrix* (Pelecanidae) and the little auk *Alle alle* (Alcidae); Harrison 1977), or single traits (e.g. bill morphology of the American redstart *Setophaga ruticilla*; Keast et al. 1995). The convergence that we found in the needle-dwellers affects a few specialised traits, namely body mass and the shape of the large digital pad on the hind toe. In contrast, the phylogenetic differences between the seven lineages pertain to numerous morphological traits of all three functional complexes. Furthermore, it is possible to almost completely separate the phylogenetic lineages from each other (Fig. 2). On the other hand, the scores of the discriminant function of “needle-dwellers” and the ones of “control species” broadly overlap, though the difference between the means is significant. This shows that in the case of needle-dwelling, the morphological adaptation is subtle but meaningful.

Specialisation for foraging in conifer needles

In contrast to our expectation, we neither found convergent patterns in the morphology of the foraging apparatus nor in the flight apparatus. In our broad

comparative approach, only the traits with the strongest correlations became significant. Biological reasons for the absence of convergence might be phylogenetic inertia and the possibility that similar problems can be solved with different responses, as, e.g., in trunk climbers (Richardson 1942; Winkler and Bock 1976). In order to climb on trunks, birds either use a supporting tail or not. The different climbing types are reflected in different morphological adaptations. Similarly, the morphological adaptations for dwelling in coniferous needles might be diverse in the feeding and flight apparatus. The feeding apparatus might correlate with the type of food taken, which is not considered in this study. Several different flight types might be used in coniferous woods: e.g. slow flights and hovering within the dense canopy, or fast flights in the open space between single trees. These different flight types may result in different morphological adaptations. However, we found a correlation between dwelling in needles and body mass as well as the morphology of the hind toe pad. The enlargement of this digital pad and the reduction of body mass are therefore homogenous trends in coniferous specialists among seven phylogenetic lineages.

Size

Needle-dwellers are characterised by small body masses. In contrast to our study, Greenberg (1979) found that conifer-dwelling *Dendroica* species are larger than their congeners in deciduous woods. This difference might be due to the use of different species and different methods of data analysis. Greenberg's study is based on 16 species, which included two large coniferous species (*D. kirtlandi*, *D. castanea*) that were not investigated in our study. On the other hand, among our 15 *Dendroica* species there are two small coniferous species (*D. occidentalis*, *D. graciae*) which are not in Greenberg's sample.

In line with our study, coniferous species tend to be smaller than deciduous species among the *Phylloscopus* warblers (Gaston 1974; Forstmeier et al. 2001). The latter authors developed three hypotheses to explain such a relationship: (1) Small species may show a preference for coniferous habitats because small body size allows more efficient use of foraging techniques that are advantageous in coniferous vegetation, such as hovering flight and clinging to conifer-needles, (2) larger species may prefer habitats with on average larger prey items, which are found in deciduous trees (Nyström 1991), and (3) smaller species might profit from the reduced inter-specific competition in a coniferous habitat (Forstmeier et al. 2001). For our study, we favour the first hypothesis, since our “needle-dwellers” prefer foraging sites that are high off the ground, and clinging to thin substrates and hovering flight are preferred locomotion types at such high foraging sites (Morse 1976; Greenberg 1979; Perrins 1979). However, we cannot exclude the other two hypotheses.

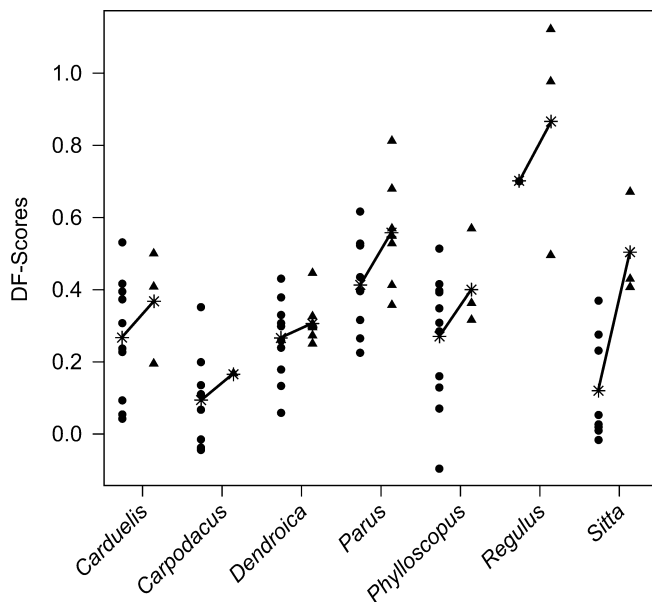


Fig. 4 The scores of the discriminant function separating needle-dwellers from the control species. Within each genus, the mean of the needle-dwellers lies higher than in the control species (the connections have all positive slopes). Filled circle control species, triangle needle-dweller, star mean

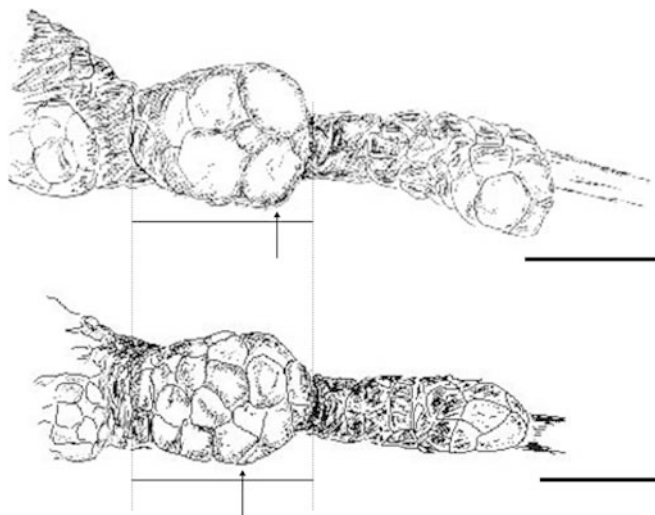


Fig. 5 Ventral view of the left hind toe of a typical needle-dweller, the goldcrest *Regulus regulus* (above), and the control-species firecrest *Regulus ignicapillus* (below). Bars 2 mm. Arrows maximum width of the proximal toe pad which lies more distally in the goldcrest than in the firecrest. From this follows a broad distal side of the goldcrest's pad. Such a pad shape may be suited to squeeze single needles between this and the adjacent (distal) pad. Hatched lines edges of the pad

Small body mass might be an adaptation for foraging in the outermost twigs of conifers for three reasons: (1) The fine structures support only small body masses, (2) on thin and elastic substrates possible bipedal locomotion types are clinging or hanging, for both of which it is advantageous to be small (Gaston 1974), and (3) resources on the outermost twigs can also be exploited by hovering, for which it is energetically better to be small (Norberg 1990).

Digital pad morphology

We interpret the high pads with distal maximal widths (Fig. 5) to be a specialisation for clinging to a thin

substrate such as needles where hanging by hooking with claws is difficult, while a frictional force between the needles and the foot is required. This function of the digital pad has already been suggested by Leisler and Thaler (1982), Winkler and Leisler (1985), and Keast and Saunders (1991) in birds and by Krättli (2001) in mammals (Muridae). Similarly, Lennerstedt (1974) found that the shapes of digital pads in passerines are highly adapted to their substrate. Pictures show that birds holding onto coniferous twigs squeeze single needles between adjacent toe pads (Winkler and Leisler 1985; Thaler-Kottek 1990; Korner-Nievergelt 2003). This, rather than a firm grip around the entire twig, seems to allow small passerines to dwell in coniferous trees. In addition, it seems plausible that a high digital pad with a distal maximal width (i.e. with a broad side towards the neighbour pad) helps to safely squeeze needles between pads. Therefore, we suggest that needle dwellers cling actively to the needles themselves, rather than only hook onto twigs as suggested by Löhrl (1974). The convergence in the digital pad morphology suggests that most birds seem to use a similar technique for pedal locomotion on coniferous needles. Our results show that convergence can affect subtle morphological traits which, nevertheless, are ecologically important.

Acknowledgements We thank the following curators for kindly providing material: M. Adams, R. van den Elzen, S. Frahnert, M. Güntert, J. Hegelbach, A. Shapoval, F. Steinheimer and R. Winkler. J. Fiebig introduced us to the helpful cherry-laurel method. Anne Thorson and Maiken Winter improved the English.

Appendix

Table 4 lists investigated species with the number of investigated specimens, and the description of their habitat with typical tree species and foraging locality

Table 4 Investigated species with the number of investigated specimens, and the description of their habitat with typical tree species and foraging locality. Bold type indicate the needle-

dwellers. If not otherwise indicated, information and systematics from: Baker 1997; Clement et al. 1993; Curson 1994; Harrap 1996 and Poole and Gill 1992-2002

Scientific name, English name and number of specimens	Habitat description	Description of foraging locality and codes of foraging habitat types according to Table 1
<i>Sitta pusilla</i> , Brown-headed nuthatch (6)	Open pine forest and pine-oak woodland, <i>Pinus taeda</i> , <i>Pinus australis</i> in winter	Forages in the treetops, near the tips of branches, less frequently on trunks and larger branches (1)
<i>S. pygmaea</i> , Pygmy nuthatch (11)	Ponderosa pine forest and pinyon-juniper woodland, <i>Pinus ponderosa</i> , <i>Pinus jeffreyi</i>	High up in the top and outer branches, in winter also on trunks and larger limbs (Stallcup 1968) (1)
<i>S. whiteheadi</i> , Corsican nuthatch (6)	Corsican pine forest, <i>Pinus nigra</i>	In needle clusters and among small branches, in winter also on trunks and larger branches (1)
<i>S. azurea</i> , Blue nuthatch (6)	Lower montane forest	Middle and upper storey of tall forests (7)

Table 4 (Contd.)

Scientific name, English name and number of specimens	Habitat description	Description of foraging locality and codes of foraging habitat types according to Table 1
<i>S. canadensis</i> , Red-breasted nuthatch (9)	Coniferous forest, spruce and fir, <i>Tsuga sp.</i> , <i>Pinus ponderosa</i>	In dense crowns of conifers, but may feed lower in trees (2, 3)
<i>S. carolinensis</i> , White-breasted nuthatch (8)	Mature open deciduous forest	On trunk and larger branches of trees, occasionally on the ground (3, 5)
<i>S. castanea</i> , Chestnut-bellied nuthatch (5)	Open dry deciduous forest	Forages in the upper half of the trees, on the trunk and smaller branches, also on the ground (3, 7)
<i>S. europea</i> , European nuthatch (13)	Deciduous and mixed forest, especially oak, <i>Quercus sp.</i>	Trunk (3)
<i>S. himalayensis</i> , White-tailed nuthatch (9)	Oak and rhododendron forest, avoids <i>Abies</i> (Martens and Eck 1995), <i>Quercus semercarpifolia</i>	Mossy branches in the upper part of the tree (5)
<i>S. magna</i> , Giant nuthatch (4)	Pine forest	Feeds on the limbs of trees, rather than on the trunk (2)
<i>S. neumayer</i> , Western rock nuthatch (6)	Rocky slopes, cliffs and gorges	On rocks and the ground (11)
<i>Parus ater</i> , Coal tit (21)	Coniferous forest (Snow 1954)	In the crown of conifers (Alatalo 1982), in the interior parts of the tree Morse 1978) (1, 2)
<i>P. cristatus</i> , Crested tit (9)	Pure stands of conifers, especially spruce and pine (Snow 1954)	In the canopy among twigs and needles (Alatalo 1982) (1, 2, 3, 8)
<i>P. gambeli</i> , Mountain chickadee (6)	Montane coniferous woodland	Among the smaller branches, sometimes probing among needle clusters at the tip of branches, foliage and twigs (1, 2, 6, 7)
<i>P. hudsonicus</i> , Boreal chickadee (6)	Dense boreal coniferous forest, conifer specialist	Among the foliage and the tips of branches in the upper part of trees, larger substrates (Sabo 1980) (1, 2)
<i>P. melanolophus</i> , Spot-winged tit (6)	Coniferous forest content also with oak (Martens and Eck 1995; Snow 1954), <i>Abies spectabilis</i> , <i>Picea smithiana</i> , <i>Pinus wallichiana</i> , <i>Cupressus torulosa</i> , <i>Quercus</i>	On the trunks or in the canopy of deciduous trees, frequently found feeding in the needles of conifers (1,3,5)
<i>P. rufescens</i> , Chestnut-backed chickadee (6)	Coniferous forest	Often high in tall conifers (Shaw and Flick 1999) (1)
<i>P. sclateri</i> , Mexican chickadee (5)	Montane coniferous forest, prefers oak to pine	Among leaves and twigs and investigates open pine cones (1)
<i>P. atricapillus</i> , Black-capped chickadee (11)	Deciduous and mixed forest (Snow 1954)	In trees and bushes, exploring the bark from the trunk to the thinnest twigs, feeds among foliage (Sturman 1968) (3, 7, 8)
<i>P. carolinensis</i> , Carolina chickadee (5)	Broadleaved woodland	Among twigs and smaller branches (4, 5)
<i>P. dichrous</i> , Grey-crested tit (7)	Wide variety of forest types (Snow 1954)	At lower and middle storeys of trees, in bushes and also on the ground (7, 8, 10)
<i>P. lugubris</i> , Sombre tit (9)	Maquis, scattered trees and bushes, olive, broadleaved woodland, farmland, oak-juniper, <i>Quercus</i> , <i>Prunus</i> , <i>Juniperus</i> , <i>Juglans</i> , <i>Rosa</i> , <i>Rubus</i> , <i>Salix</i> (Catsadorakis and Källander 1999; Snow 1954)	On the lower branches of trees and in the shrub layer, sometimes on the ground (8)
<i>P. montanus</i> , Willow tit (12)	In western Europe: willow, alder, birch, in Scandinavia: coniferous forest	Favours the herb and shrub layers and the lower branches and foliage of trees (Alatalo 1982) (6, 7, 8, 9)
<i>P. palustris</i> , Marsh tit (13)	Mature deciduous forest (Snow 1954)	All levels of vegetation; in the outer portions of the branches (Morse 1978), preference for bushes and lower branches of trees, in winter on the ground, 60% in branches (Suhonen et al. 1994) (4, 5, 8, 10)
<i>P. rubidiventris</i> , Rufous-bellied tit (8)	Variety of forest types, <i>Abies spectabilis</i>	Largely in the canopy, also in the shrub layer (6, 7, 8)

Table 4 (Contd.)

Scientific name, English name and number of specimens	Habitat description	Description of foraging locality and codes of foraging habitat types according to Table 1
<i>P. rufonuchalis</i> , Rufous-naped tit (9)	Spruce, fir and cedar forest, dry forest, nearly exclusively conifers (Martens and Eck 1995), open forest, <i>Pinus wallichiana</i> , <i>Abies spectabilis</i> , <i>Picea smithiana</i>	In the canopy, shrub layer and on the ground (2, 8, 10)
<i>Regulus calendula</i> , Ruby-crowned kinglet (7)	Coniferous and mixed forest, affinity for spruce, spruce (Kessel 1998)	According to Sabo (1980) higher up in the canopy than <i>R. satrapa</i> (1)
<i>R. regulus</i> , Goldcrest (11)	Coniferous forest the year round (Martens and Eck 1995), <i>Pinus</i> , <i>Abies</i>	Canopy, rather tit-like among needles (Alatalo 1982) (1)
<i>R. satrapa</i> , Golden-crowned kinglet (6)	Coniferous forest	Canopy, among needles, conifer specialist using fine substrate (Sabot 1980) (1)
<i>R. ignicapillus</i> , Firecrest (10)	Lowland broadleaved and mixed forest	Canopy (5, 7)
<i>Phylloscopus proregulus</i> , Palla's leaf warbler (8)	Tall conifer forests with dense scrub undergrowth, no special preference (Martens and Eck 1995), <i>Abies</i> , <i>Tsuga</i> , <i>Quercus semecarpifolia</i> , <i>Betula</i> , <i>Picea</i> , <i>Pinus</i>	In canopy, goldcrest-like on the outside of trees, also often found in the bottom stratum., among the low shrubbery at the edge of the forest (Martens and Eck 1995) (1, 2)
<i>P. pulcher</i> , Orange-barred leaf warbler (10)	Conifer, or mixed conifer forest, preference for close stands (Martens and Eck 1995), <i>Abies spectabilis</i> , <i>Abies densa</i> , <i>Betula utilis</i> , <i>Juniperus</i>	In tree canopy, among foliage (1, 2)
<i>P. subviridis</i> , Brook's leaf warbler (6)	Conifer forests, such as spruce, fir and pine	Canopy, among foliage (1, 2)
<i>P. tytleri</i> , Tytler's leaf warbler (5)	Coniferous forest such as blue pine and silver fir	Outer boughs of fir or pine trees, or amongst the branches of dwarf willow, arboreal deciduous/conifers (Gaston 1974) (1, 2, 4)
<i>P. bonelli</i> , Western Bonelli's warbler (6)	Open deciduous woodlands, also mixed or pure coniferous stands	In foliage (2, 6)
<i>P. collybita</i> , Chiffchaff (12)	Open mature forests of conifers, mixed and broadleaf varieties	In foliage, from ground level up to tree canopy (6, 7, 10)
<i>P. coronatus</i> , Eastern crowned leaf warbler (6)	Mixed or deciduous open woodland	Arboreal, but forages at all levels (6, 7, 8)
<i>P. (inornatus) humei</i> , Hume's leaf warbler (9)	Lightly forested hills, especially silver fir, larch and pine-cedar	At all levels, also shrubs, among foliage (Gross and Price 2000) (6, 7, 8)
<i>P. inornatus</i> , Yellow-browed warbler (7)	Open growth of broadleaved trees and shrubs	At all levels of the trees, among foliage (4, 5, 8)
<i>P. maculipennis</i> , Ashy-throated leaf warbler (6)	Open, mixed forests of oak and rhododendron or conifer, no discernible preferences (Martens and Eck 1995)	Strongly arboreal (6, 7, 8)
<i>P. magnirostris</i> , Large-billed leaf warbler (6)	Open grassy glades, open spaces with fallen trees, closely associated with fast-flowing noisy mountain brooks, no preference for any forest type (Martens and Eck 1995)	Lower branches of firs, undergrowth, among low vegetation on grassy banks (2, 7)
<i>P. neglectus</i> , Plain leaf warbler (6)	Thickets of juniper and pistachio, and open degraded oak woods	Essentially arboreal (6, 7, 8)
<i>P. reguloides</i> , Blyth's leaf warbler (6)	Mountain forests of conifer or mixed deciduous stands, high ecological plasticity (Martens and Eck 1995)	Canopy, secondary scrub and bush layer (4, 6, 8)
<i>P. schwarzi</i> , Radde's warbler (5)	Tall herbage, thick scrub layer	On the ground (8, 10)
<i>P. sibilatrix</i> , Wood warbler (7)	All types of forests offering continuous canopy and open or sparse vegetation	In tree canopies (7)
<i>P. subaffinis (affinis)</i> , Buff-throated warbler (5)	Alpine scrub and forest edges, bushes, dry habitat (Martens and Eck 1995)	On the ground, thick vegetation (8, 9, 10)
<i>P. tenellipes</i> , Pale-legged leaf warbler (6)	Dense, often moist broadleaf and mixed forests in river valleys	Middle and lower storey of forest (6, 7, 8)
<i>P. trochilus</i> , Willow warbler (10)	Broad range of habitats, broadleaved woodland, open grass downland with scrub and bushy areas, gardens (Bibby et al. 1985)	In foliage, (Alatalo 1982), from ground level up to tree canopy (4, 6, 7, 10)

Table 4 (Contd.)

Scientific name, English name and number of specimens	Habitat description	Description of foraging locality and codes of foraging habitat types according to Table 1
<i>Carduelis monguilloti</i> , Vietnamese greenfinch (6)	Open wooded areas of <i>Pinus insularis</i> , <i>Pinus insularis</i>	Canopy (1, 2, 13)
<i>C. pinus</i> , Pine siskin (6)	Conifers, mainly spruce, mixed forest	Feeds on a variety of seeds (1, 4, 6, 10)
<i>C. spinus</i> , Siskin (12)	Conifers, chiefly spruce, also in alders, larch and beech	High up in conifers, also on ground (1, 2)
<i>C. barbata</i> , Black chinned siskin (6)	Forests to open country	Mostly on the ground, also high in trees (7, 9, 10)
<i>C. cannabina</i> , Linnet (10)	Heathland with scattered trees	Ground (9, 10)
<i>C. carduelis</i> , Goldfinch (8)	Variety of habitats	On plants or on the ground (9)
<i>C. chloris</i> , Greenfinch (13)	Low forests, orchards, and gardens	Ground-loving forager (5, 9, 10)
<i>C. flammea</i> , Common redpoll (9)	Open subarctic, largely coniferous forest	On alders or birch catkins, plants and on the ground; feeds in trees and shrubs at ends of small branches, 96% in vegetation, 5% on ground (4, 8, 9, 10)
<i>C. flavirostris</i> , Twite (8)	Open hillsides, moorland, open terrain or cliffs	Ground, or on vegetation (9, 10, 11)
<i>C. hornemanni</i> , Arctic redpoll (5)	High arctic, tundra, ravines, slopes, dwarf birch and willow thickets	Feeds actively in trees, often at extremities, searches stems and crotches for insects, on the ground (8)
<i>C. notata</i> , Black-headed siskin (4)	Conifer and oak forest	Small plants, pines (9)
<i>C. psaltria</i> , Dark-backed goldfinch, Lesser goldfinch (6)	Dry, open country, brush, woodland or roadside edges, <i>Pinus-Juniperus</i> , <i>Populus fremontii</i> , <i>Salix nigra</i>	Feeds on a variety of seeds from trees, sunflowers and on the ground (4, 9)
<i>C. spinoides</i> , Himalayan greenfinch (5)	Oak, rhododendron or conifer forest, no preference for either coniferous or broad-leaved trees (Martens and Eck 1995)	At the top of pines or alders (6, 7, 8)
<i>Carpodacus cassinii</i> , Cassin's finch (6)	Open conifer forest, <i>Pinus contorta</i> , <i>P. ponderosa</i>	Feeds either in the top of tree or on the ground, removes seeds from cones and insects from conifer foliage (Torgersen et al. 1990) (1, 10)
<i>C. erythrinus</i> , Common rosefinch (8)	Willow or tamarisks, thickets or patches of scrub or bushes, pines and firs nearby (Martens and Eck 1995)	Plant and tree seeds and buds, bamboo, crops (7, 8, 9)
<i>C. mexicanus</i> , House finch (7)	Suburban towns, villages, farmland, desert, grassland	Spends more time on ground than other <i>Carpodacus</i> (10)
<i>C. nipalensis</i> , Dark rosefinch (6)	Mixed oak or conifer and rhododendron forest, <i>Rhododendron</i> (Martens and Eck 1995)	Feeds on small seeds, also nectar from rhododendron (8, 9)
<i>C. pulcherrimus</i> , Beautiful rosefinch (12)	Rhododendron, buckthorn, oak and juniper scrub and forest edges, coniferous zone (Martens and Eck 1995)	Low down or on the ground (8, 10)
<i>C. puniceus</i> , Red-breasted rosefinch (4)	Alpine meadows, plateaus, dry valleys, rock screes, cliffs and glaciers	Ground (10)
<i>C. purpureus</i> , Purple finch (7)	Conifer forest	Outer portions of tree branches, bushes or on the ground (2, 8, 10)
<i>C. roseus</i> , Pallas's rosefinch (5)	Conifer, birch and cedar forest	In trees, bushes or on the ground (2, 7, 9)
<i>C. rubicilla</i> , Caucasian great rosefinch (5)	High-altitude valleys and plateaus of open boulder or rock-strewn areas	Feeds on the ground or in bushes (8, 10)
<i>Dendroica fusca</i> , Blackburnian warbler (5)	Mature coniferous forest and mixed forest, hemlock	High in canopy, on small limbs (Morse 1968) (1, 13)
<i>D. graciae</i> , Grace's warbler (5)	Pine-oak forest, Ponderosa pine, yellow pine	Treetops, high levels (1, 6, 13)
<i>D. magnolia</i> , Magnolia warbler (12)	Coniferous forest, young stands of spruce, balsam fir or hemlock, <i>Pinus strobus</i>	Low to middle levels, midstory (Sabo 1980), on small limbs (Morse 1968), on outer ends of branches at midtree heights in dense conifer foliage, also in dense broadleaved shrubs (1, 2, 13)
<i>D. occidentalis</i> , Hermit warbler (5)	Tall mature coniferous forest, Douglas fir, <i>Abies</i> , <i>Picea</i>	Treetops, concentrates activity on foliage and twigs (1)

Table 4 (Contd.)

Scientific name, English name and number of specimens	Habitat description	Description of foraging locality and codes of foraging habitat types according to Table 1
<i>D. pinus</i> , Pine warbler (8)	Pine forest, exclusively pines, <i>Pinus taeda</i>	Distal half of limb and tips of foliage (Ficken et al. 1968), foraging observations: 43% in pine foliage, 30% bark, 13% air (1, 2, 10)
<i>D. tigrina</i> , Cape May warbler (6)	Black spruce forest, black spruce	High in the trees, in rainy weather in thickets of willows (MacArthur 1958) (1, 13)
<i>D. townsendi</i> , Townsend's warbler (6)	Tall mature coniferous forest, especially fir, <i>Picea glauca</i> (Matsuoka et al. 1997), <i>Pseudotsuga menziesii</i> (Marzluff et al. 1996)	Treetop, on migration often near the ground (Tramer and Kemp 1982) (1, 13)
<i>D. caerulescens</i> , Black-throated blue warbler (7)	Mature deciduous and mixed woodland	In the understory and on the ground, lower to mid strata (7, 8)
<i>D. cerulea</i> , Cerulean warbler (6)	Mature deciduous, tall trees, occasionally mixed woods	Mainly in the canopy, takes food from leaf bases and foliage (4, 13)
<i>D. coronata</i> , Yellow-rumped warbler, Myrtle (9)	Coniferous or mixed forest or woodland	Mostly at high levels, also on trunks and branches (Sabo 1980), on small limbs (Morse 1968), often from lower branches, often clings to vertical bark (6, 7, 13)
<i>D. palmarum</i> , Palm warbler (7)	Bogs, especially spruce bogs, but avoids dense forest, <i>Picea mariana</i> , <i>Larix laricina</i>	Ground (77% on ground, 15% in air, 9% on broad leaves (Lack and Lack 1972 in Poole and Gill 1992–2002) (10)
<i>D. pensylvanica</i> , Chestnut-sided warbler (5)	Young second-growth deciduous forest, brushy thickets	At low to middle levels in shrubs and the lower branches of tall trees (5)
<i>D. petechia</i> , Yellow warbler (10)	Open, often damp habitats such as alder and willow thickets	From the ground to the treetops, never on ground, on small limbs (6, 7, 10, 13)
<i>D. striata</i> , Blackpoll warbler (5)	Spruce forest, <i>Picea mariana</i> , <i>Abies balsamea</i>	At mid to high level, midstorey (Sabo 1980), inner branches (Morse 1979), often seen probing in closed buds on twigs (2, 13)
<i>D. virens</i> , Black-throated green warbler (7)	Open coniferous and mixed forest	All levels (Maurer and Whitmore 1981; Tramer and Kemp 1982; Sabo 1980), small limbs (Morse 1968) (6, 7, 13)
<i>Parula americana</i> , Northern parula (8)	Deciduous or coniferous forest, <i>Usnea</i> lichen	Treetops (6)
<i>P. pitaiayumi</i> , Tropical parula, Olive-backed warbler (7)	Deciduous and gallery forest, oak woodland with epiphytes, ball moss <i>Tillandsia baileyi</i>	Mainly in the outer branches of the canopy, tends to forage near ends of branches of twigs (4, 6)
<i>P. superciliosa</i> , Crescent-chested warbler (3)	Pine-oak and cloud forest	Middle to high levels (4, 5, 6)

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